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DICOTYLEDONOUS WOOD FROM THE UPPER CRETACEOUS OF CENTRAL CALIFORNIA

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THE CRETACEOUS is well represented in California by extensive marine sediments, known as the Great Valley Sequence, exposed along the western border of the Central Valley. Wood occurs in limited quantities in the sequence from the Aptian through the uppermost stages. Wood also occurs in relative abundance throughout the Tertiary in all of the far western states; thus, a unique opportunity is available for the study of compositional and pattern changes encompassing a long span of time. With one exception (CASG 59858, of unconfirmed provenance¹), the few wood specimens examined so far from Lower Cretaceous localities are gymnosperms; however, angiosperms may have been in the region by Albian time, as this sample indicates. They were certainly in the region by the Coniacian, as a specimen to be described indicates, and by Maastrichtian time angiosperms were diverse and relatively abundant, as shown not only by remains of wood but particularly by pollen (Chmura, 1973; Drugg, 1967). The present report is the first of a series summarizing the results of an investigation of a suite of fossil woods collected from the upper portions of the Great Valley Sequence. Among the samples showing sufficient anatomical structure, there are over sixty dicotyledons, fifteen gymnosperms, and one monocotyledon. Descriptions of ten dicots and one gymnosperm have been published elsewhere (Page, 1967, 1968, 1970, 1973).

GEOLOGIC OCCURRENCE AND AGE

The specimens to be described were collected from five localities. Since two of these sites are not represented in this first paper, a description of them will be presented when the specimens obtained from them are discussed. The assemblage to be described here was derived from weathered

¹This specimen was found among the geological collections of the California Academy of Sciences. It was collected in 1929 by F. M. Anderson. According to his label, the locality is in the Chickabally Member of the Horsetown Formation. The age of this member is Aptian-Albian.

mudstone at three localities in the foothills of the Diablo Range, west of the town of Patterson in Stanislaus County. The specimens occur sporadically, together with gypsum-encrusted phosphatic concretions that contain a rich assortment of pollen, spores, radiolarians, foraminifera, dinoflagellates, and other microfossils. The specific locations are as follows:

Locality 1. Del Puerto Creek; SE $\frac{1}{4}$ SW $\frac{1}{4}$ sect. 20, R. 7 E., T. 5 S., Oristimba 15" quadrangle.

Locality 2a. Black Gulch; NE $\frac{1}{4}$ SE $\frac{1}{4}$ sect. 32, R. 7 E., T. 5 S., Oristimba 15" quadrangle.

Locality 2b. Unnamed; NW $\frac{1}{4}$ NW $\frac{1}{4}$ sect. 4, R. 7 E., T. 5 S., Oristimba 15" quadrangle.

Locality 2b lies about three-eighths of a mile south of locality 2a. The two sites lie on strike and are essentially time equivalent (J. Stein, pers. comm.). Locality 1 lies about two and one-quarter miles to the northwest of locality 2b and slightly oblique to regional strike. Chmura (1973) places locality 1 stratigraphically above locality 2a (and therefore 2b as well) and estimates the stratigraphic distance to be about 1200 feet (365 m.).

Chmura (1973), citing Bishop (1970 and pers. comm.), assigns locality 1 to the Maastrichtian on the basis of foraminiferal fauna that indicate a "C and/or D-1" zone of Goudkoff (1945). Again citing personal communication with Bishop, Chmura reports his opinion that locality 2 falls within Goudkoff's D-2 zone and is, therefore, Campanian. Most workers, however, place the boundary between the Maastrichtian and the Campanian below the D-2 zone. Acceptance of this latter interpretation would place localities 2a and 2b in the Maastrichtian. Recent work on dinoflagellate assemblages from each of the three localities has confirmed the occurrence of a typical Maastrichtian dinoflagellate assemblage in all three (J. Stein, unpubl.).

Ingersoll (1976) has described the Great Valley Sequence as a series of subsea fan deposits, and localities similar to the above as probably basinal facies. Since this mode of deposition has great bearing on assessments of the ecological and evolutionary significance of the suite of fossils to be described, it will be discussed more fully later.

SYSTEMATICS

Fossil woods have long been the despair of paleobotanists because of the many problems associated with attempts to find modern correlatives. Despite the seemingly insurmountable obstacles, these fossils remain an excellent source of information about past vegetation. The stem is an important part of the plant. It is reasonable to suppose that this has always been so; therefore, the evolutionary history of the stem is as essential as that of any other part of the plant in our search for answers to the question of the origin of the angiosperms and their subsequent diversification.

Moreover, although evolutionary pathways can be inferred from the study of modern woods, as I. W. Bailey and his students have shown, the rate and extent of specialization in the past can be known only from the fossil record. The kinds of facts needed for this aspect of paleobotany can (and should) be obtained independently of reference to presumed relationships of fossils to modern taxa.

The factors that contribute to frustration in dealing with fossil woods are numerous and stem chiefly from three sources: state of preservation, serious gaps in our knowledge of modern woods, and age of the fossils. Fossils are organisms or parts of organisms that have, for the time being, partially or completely escaped the recycling process that is a fundamental part of nature. The state of preservation of such relics varies according to the amount and kind of degradation that preceded mineralization, to the degree of distortion due to the pressure of the overlying rock burden, and to other post-depositional physical and chemical processes. Of the characters most likely to be preserved in secondary xylem, the most important are: distribution of the various cellular components, size of the vessel elements, type of perforation plate, type of intervessel pitting, ray structure, fiber structure, and presence and distribution of tracheids, included phloem, oil cells, resin or gum ducts, and crystals. Unfortunately, circumstances leading to the final condition of preservation too often obscure or obliterate some essential features. Although the presence of a particular feature can be demonstrated, the fact of primal absence can not always be assumed if it can not be observed. For example, in specimens with scalariform end plates averaging less than 20 bars, there are times when it is not possible to be certain that all plates were scalariform, particularly if the vessels are filled with tyloses. Distortion of the grain due to pressure often obscures or alters the appearance of rays, the presence of growth rings, and the distribution of parenchyma and vessels. Degradation by microorganisms may destroy essential components of either the primary or the secondary wall of cells. In some cases nothing remains of the cells but the middle lamella or the primary walls, while in others the primary walls have largely disappeared, leaving only secondary walls. Needless to say, such structures as wall pitting and bars of perforation plates, not to mention spiral thickening and fiber septae, may be greatly altered by the disintegration of either the primary or the secondary wall. Provided that a sufficient amount of wall material of any kind remains, the presence or absence of wall pits or perforation plate bars is not affected; the effect is on the border in the case of pits, and on the thickness of bars in the case of perforation plates. Important features such as the arrangement of pits and the number of bars in the end plates may still be preserved.

Even when we are fortunate enough to have well-preserved specimens, we are faced with important gaps in our knowledge of modern woods. One of the more serious problems encountered in evaluating the assemblage to be described is that 70 percent of the specimens are small branches or roots, less than five centimeters in diameter. It is well known

that in woody dicots the early increments of secondary xylem are often structurally different from those in later-formed wood (Bailey & Tupper, 1918), and that the duration of the early or immature stage varies among genera (Bailey, 1924). Because of the changes that take place before structural features become established, most descriptive studies are based on mature woods. Very little, therefore, is known about the duration and kinds of changes that occur during maturation of the stem or root of any one genus. These gaps in our knowledge present serious obstacles in the way of efforts to find modern counterparts of fossilized branch or root material unless distinctive structures are present in the fossils. The presence of pith or bark is of little assistance because our knowledge of these tissues is totally inadequate for the purpose of comparative studies.

Other variables that must be considered and about which information is limited are those arising from differences that may exist in mature secondary xylem from different parts of the plant, for example, reaction wood or crotch wood (summarized in Carlquist, 1961). Unless the primary xylem is present, there is no way of knowing whether a sample of petrified wood is from a root or a stem. Such characters as pore distribution, ray structure, growth rings, and amount and distribution of parenchyma may differ widely between root and stem of the same plant. Similarly, the length of vessel elements and fibers, as well as the structure of rays, may vary considerably from the normal in and around the fork of a branching system. Ecological factors often affect the diameter and frequency of vessels as well as the presence or absence of spiral thickening among related species or among individuals of the same species (summarized in Carlquist, 1975). These kinds of variation are seldom included in descriptions of wood. Finally, because most research on wood has been performed for the purpose of identifying or determining the properties of commercially important timbers, information about the large number of noncommercial woods is limited. Although there has been a renewed interest in comparative anatomy in recent years, relatively few families have been analyzed in detail, so such important information as the ranges of variation within and among families is scanty. Because of circumstances of availability, size of the wood specimen, and the amount actually examined, it can seldom be said that the fossil material examined in detail by an investigator represents an adequate sampling of the species from which a particular specimen was derived. Since variation occurs not only within a species today but also within a given individual, it is unwise to assume that these fossils are typical of the species they now represent.

Can we assume that the species or genus or family even exists today? If the concept of organic evolution has any validity in fact, one would expect many changes to have taken place among the dicots since the close of the Cretaceous period. That changes have occurred is indicated by the experience of many paleobotanists working with plant organs from the early Tertiary or older strata. A particularly illustrative case is that of the Eocene London Clay flora (Reid & Chandler, 1933). Although the fossil

assemblage consists of a variety of plant parts, the important constituents and the ones that have been thoroughly investigated are fruits and seeds; thus, it would present a better picture of the relationship with modern taxa as they are circumscribed than would assemblages of wood or leaves. The authors found that two-thirds of the genera they recognized cannot be aligned with modern genera. Moreover, in a perusal of Chandler's summary (1964), I observed that about 15 percent of the angiosperms listed for the early Eocene of southern England could not be placed in a modern family, and about 47 percent could be accommodated in families but not in extant genera. The remaining 32 percent closely resembled fruits and seeds of modern genera but were unlike any modern species. It is not unreasonable to assume that the percentage of extinct genera would be greater among Late Cretaceous fossil assemblages.

Recently, the attention of plant anatomists (see Braun, 1970; Baas, 1973; Carlquist, 1975) has been focused on the relationship between physiological requirements of the plant and structure of its wood. Carlquist (1975) suggests that not only is there a close correlation between structure and habitat, but that evolutionary changes in angiosperms as a whole have been affected by responses to changes in the environment. In light of this idea, similarities I have observed in woods of certain species in such families as the Lauraceae, Leguminosae, Combretaceae, Moraceae, and Anacardiaceae may be attributed to similarity in responses to ecological factors. The basic pattern common to these families (simple perforation plates, alternate intervessel pits, slightly heterogeneous rays, paratracheal parenchyma, septate fibers) is modified in similar directions. In all the groupings the tendency is toward amplification of axial parenchyma, and toward storeying of elements. One can ask whether these similarities reflect genetic relationship or merely a similarity in adaptive responses. That genetic affinities probably do not account for the similarities is indicated by phylogenetic schemes based on reproductive structures primarily (Cronquist, 1968) and on leaves (Hickey & Wolfe, 1975). In both systems, not only is each family mentioned above placed in a different order, but at least three subclasses are represented (Hickey and Wolfe differ from Cronquist in the placement of the Myrtales, although all three authors agree that the family Combretaceae belongs to this order). The basic pattern described above may be considered a common type of alteration from the unspecialized multiperforate condition and regarded as a stage in an evolutionary sequence. Such a sequence from a generalized multiperforate condition to simple perforations with concomitant qualitative and quantitative changes in other cellular components can be observed not only in many orders of dicots but also within families — for example, the Icacinaceae, Dilleniaceae, Araliaceae, and Cunoniaceae.

Because many plant groups have responded to environmental conditions in similar ways (one result of which is closely similar wood patterns), and there is no reason to believe that this phenomenon is of recent origin, it is my opinion that one should be wary of relying on similarity alone as a criterion for judging whether a fragment of fossil wood represents a par-

ticular modern taxon. Although I advocate great caution in identifying Cretaceous woods with modern forms, I am fully aware that in dealing with any one specimen there may be a 40 percent chance that it belongs to a modern genus; however, there is also a 60 percent chance that it does not. It is essential, therefore, that we look at the fossil record unbiased by schemes of classification based on floral parts alone. One wishes to know how far back in time modern taxa can be traced, but incautious assumptions may only serve to obscure their evolutionary history.

In view of the prevalence of parallel evolution in wood patterns and the possibility that most modern genera and many families were not in existence in the Upper Cretaceous, it seems clear that taxonomic circumscriptions of extant groupings at the genus or family level should not be applied to dispersed Cretaceous plant fragments. Because of the formidable obstacles outlined above, it is particularly important to consider an alternative procedure for evaluating the relationship between Cretaceous and modern woods. The procedure adopted here is such an alternative and consists simply of a reclassification of modern woods solely on the basis of anatomical characteristics. The result is an artificial system that does not necessarily coincide with distinctions based on floral parts. Generalized patterns, such as those observed in the majority of specimens in the Cretaceous assemblage to be described, reflect a continuum of variation within and among taxa. This continuum is reticular rather than linear. Overlapping and convergence of ranges of variation are common, often among unrelated genera. There are a few basic combinations of primitive, relatively primitive, or otherwise unspecialized wood patterns shared by a large number of genera of varying degrees of relationship.

Because information about wood patterns in many modern genera is lacking or unavailable, it is not possible at the present time to construct a classification complete enough to permit recognition of lower-order-form taxa; therefore, I prefer not to give formal recognition to the groupings of fossils described here. For the present, reference to an individual specimen will be by its accession number. To provide a temporary frame of reference, modern woods (570 genera representing 158 families) were classified on the basis of the information available to me. The characters used in this classification are those most likely to be included in descriptions or to be preserved in fossils. The major groupings and their characteristics are presented below in the form of a synoptical key.

A CLASSIFICATION OF THE SECONDARY XYLEM OF DICOTYLEDONS

- | | |
|-------------------------------------------------------|-----------|
| Vessels absent. | Group I. |
| Vessels present. | |
| Perforation plates scalariform. | |
| Pores mostly solitary. | |
| Bars in perforation plates average more than 50. | Group II. |

Parenchyma sparse or absent.	IIA.
Parenchyma apotracheal only.	IIB.
Paratracheal parenchyma present.	IIC.
Bars in perforation plates average fewer than 50.	Group III.
Parenchyma sparse or absent.	IIIA.
Intervessel pits scalariform.	IIIA sect. 1.
Intervessel pits transitional/opposite.	IIIA sect. 2.
Intervessel pits opposite-alternate.	IIIA sect. 3.
Intervessel pits alternate.	IIIA sect. 4.
Parenchyma mostly apotracheal.	IIIB.
Intervessel pits scalariform.	IIIB sect. 1.
Intervessel pits transitional/opposite.	IIIB sect. 2.
Intervessel pits opposite-alternate.	IIIB sect. 3.
Intervessel pits alternate.	IIIB sect. 4.
Paratracheal parenchyma present.	IIIC.
Intervessel pits scalariform.	IIIC sect. 1.
Intervessel pits transitional/opposite.	IIIC sect. 2.
Intervessel pits opposite-alternate.	IIIC sect. 3.
Intervessel pits alternate.	IIIC sect. 4.
Pores in multiples as well as solitary.	
Bars in perforation plates average more than 50.	Group IV.
Parenchyma sparse or absent.	IVA.
Parenchyma apotracheal only.	IVB.
Paratracheal parenchyma present.	IVC.
Bars in perforation plates average fewer than 50.	Group V.
Parenchyma sparse or absent.	VA.
Parenchyma apotracheal only.	VB.
Paratracheal parenchyma present.	VC.
Perforation plates simple and scalariform.	
Pores mostly solitary.	Group VI.
Parenchyma sparse or absent.	VIA.
Parenchyma apotracheal only.	VIB.
Paratracheal parenchyma present.	VIC.
Pores in multiples as well as solitary.	Group VII.
Parenchyma sparse or absent.	VIIA.
Parenchyma apotracheal only.	VIIIB.
Paratracheal parenchyma present.	VIIIC.
Perforation plates simple.	
Intervessel pits scalariform, transitional, or opposite.	Group VIII.
Parenchyma sparse or absent.	VIIIA.
Parenchyma apotracheal only.	VIIIB.
Paratracheal parenchyma present.	VIIIC.
Intervessel pits alternate.	
Parenchyma sparse or absent.	Group IX.
Parenchyma more or less abundant.	
Parenchyma apotracheal only.	Group X.
Parenchyma diffuse.	XA.
Parenchyma banded or terminal.	XB.
Paratracheal parenchyma present.	Group XI.
Parenchyma vasicentric.	XIA.
Parenchyma aliform and/or confluent.	XIB.

SYSTEMATIC DESCRIPTIONS

Microscopic details of the fossils were obtained from thin sections. In the descriptions to follow, the omission of a feature of diagnostic importance means that it was not possible to observe that feature. In many specimens it was not possible to obtain a statistically significant reading of the number of vessels in a square millimeter because of distortion of the tissues; therefore, this feature has not been included. In a general way the relative frequency of pores can be inferred from the illustrations. The length of vessel elements was calculated by measuring the distance between outer limits of perforation plates except in instances where the end walls were clearly visible. An effort was made to obtain at least ten measurements of pore size and vessel element length for each specimen. The term "pore" is used in reference to the vessel as it appears in transverse section. The term "fiber" is used in its generic sense as defined in the *Multilingual Glossary of Terms Used in Wood Anatomy* (1964).

All thin sections are deposited in the Geological Collections of the California Academy of Sciences in San Francisco (CASG).

The specimens to be described in the first paper are classified in groups I, II, and III.

Group I is represented by two specimens, both of which were collected from locality 1. *Tetracentronites panochensis* has been described elsewhere (Page, 1968). Vesselless secondary xylem occurs in ten modern genera and five families.

CASG 60116

FIGURES 1, 2, 4.

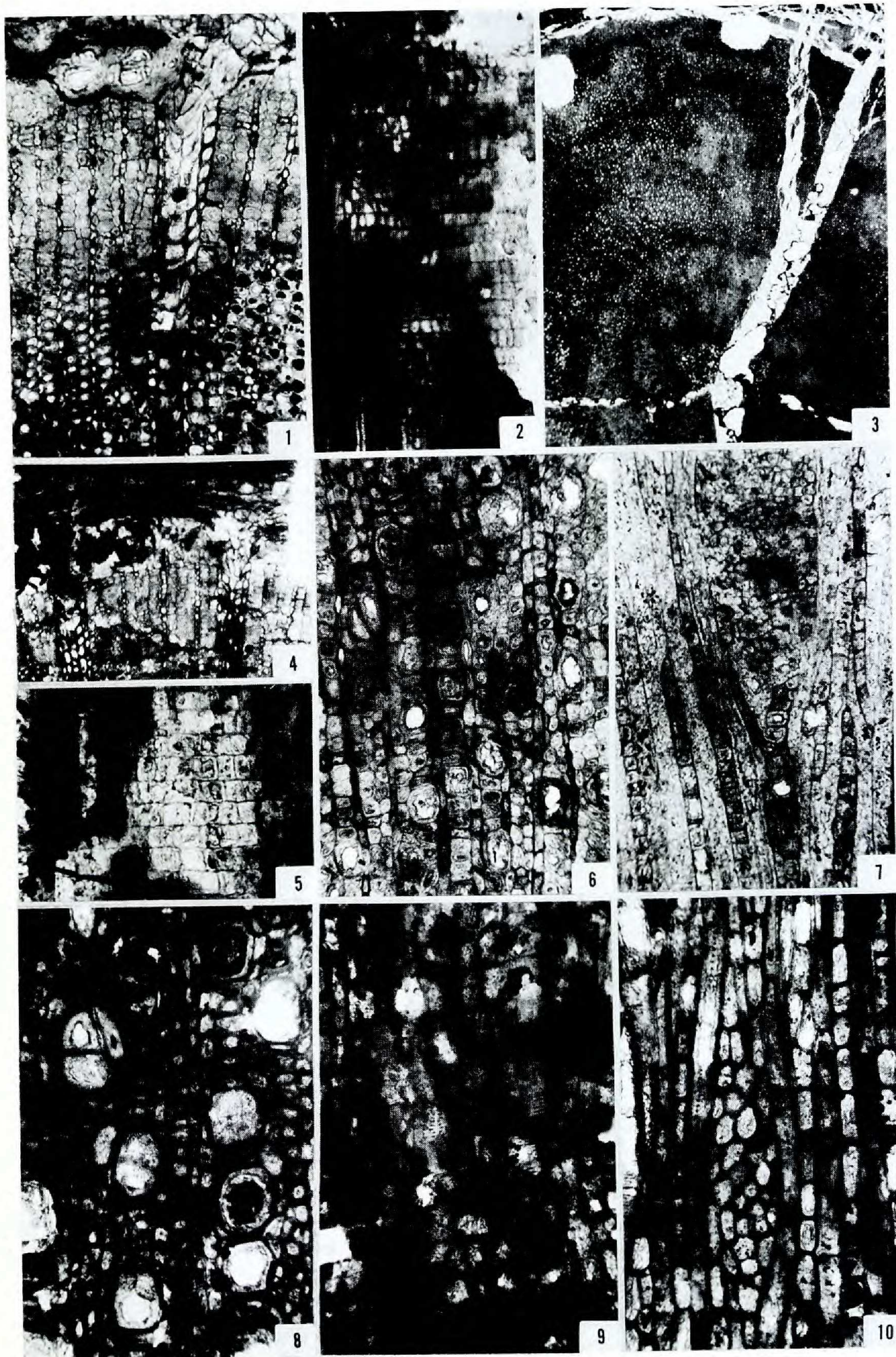
MATERIAL. Small twig about 7 mm. in diameter. Growth rings not apparent.

Secondary xylem. Vessels lacking. Tracheids small, thick walled, average diameter 26 μm . (13–38). Pits small, round; pits to ray cells somewhat larger. Parenchyma abundant. Rays uniseriate and multiseriate, the latter 4 or 5 cells wide, the cells square or upright, thick walled, with minute pits on tangential walls. Multiseriates originate at pith. Uniseriates numerous, the cells high, upright.

Pith. Appears to be homogeneous; cells large.

Phloem. Multiseriate rays flare out slightly. Outer phloem or cortex with a more or less continuous ring of a variety of sclereids.

FIGURES 1–10. 1, 2, 4, CASG 60116: 1, transverse section, $\times 70$; 2, radial section, $\times 47$; 4, transverse section showing phloem, $\times 47$. 3, 5–7, CASG 60117: 3, transverse section, $\times 4$; 5, radial section showing square cells of ray, $\times 70$; 6, transverse section, $\times 70$; 7, tangential section showing uniseriate rays and portion of large ray, $\times 70$. 8–10, CASG 60119: 8, transverse section, $\times 80$; 9, radial section (note ray pits), $\times 80$; 10, tangential section, $\times 80$.



LOCALITY. Del Puerto Creek, locality 1.

A true tangential section was not obtained. As far as can be determined, the general structure is most like that of Old World Winteraceae. New World species, as well as *Tetracentron*, *Amborella*, and *Sarcandra*, have little or no parenchyma. This fossil differs from *Tetracentronites panochensis* Page in its narrower rays, abundant parenchyma, and round pits. Because of poor preservation, pitting can be observed in only a few tracheids. Some modern species of Winteraceae produce small, round pits in narrow tracheids and scalariform pits in wide tracheids, while others produce only round pits regardless of the diameter of the cell (Carlquist, 1975). It is possible that later-formed tracheids (if the stem produced additional xylem increments) may have borne scalariform pits. *Trochodendron* has some axial parenchyma, but in mature wood the cells of the multiseriate portion of rays are procumbent and tracheids in early wood have scalariform pits. Information about young stems was not available.

The next five specimens are classified in Group II. The first, CASG 60120, falls in IIA and has septate fibers and vessel elements averaging less than 1 mm. in length. A similar pattern can be observed in the genus *Illicium* (Illiciaceae) and in *Matthaea* (Monimiaceae). The next four specimens (CASG 60117, CASG 60118, CASG 60119, and CASG 60130) fall in IIB. All have vessel elements over 1 mm. in length. Modern woods that are classified as Group IIB and that have this characteristic occur in such families as the Cornaceae, Theaceae, Dilleniaceae, Nyssaceae, Icacinaceae, Aquifoliaceae, Symplocaceae, and Clethraceae.

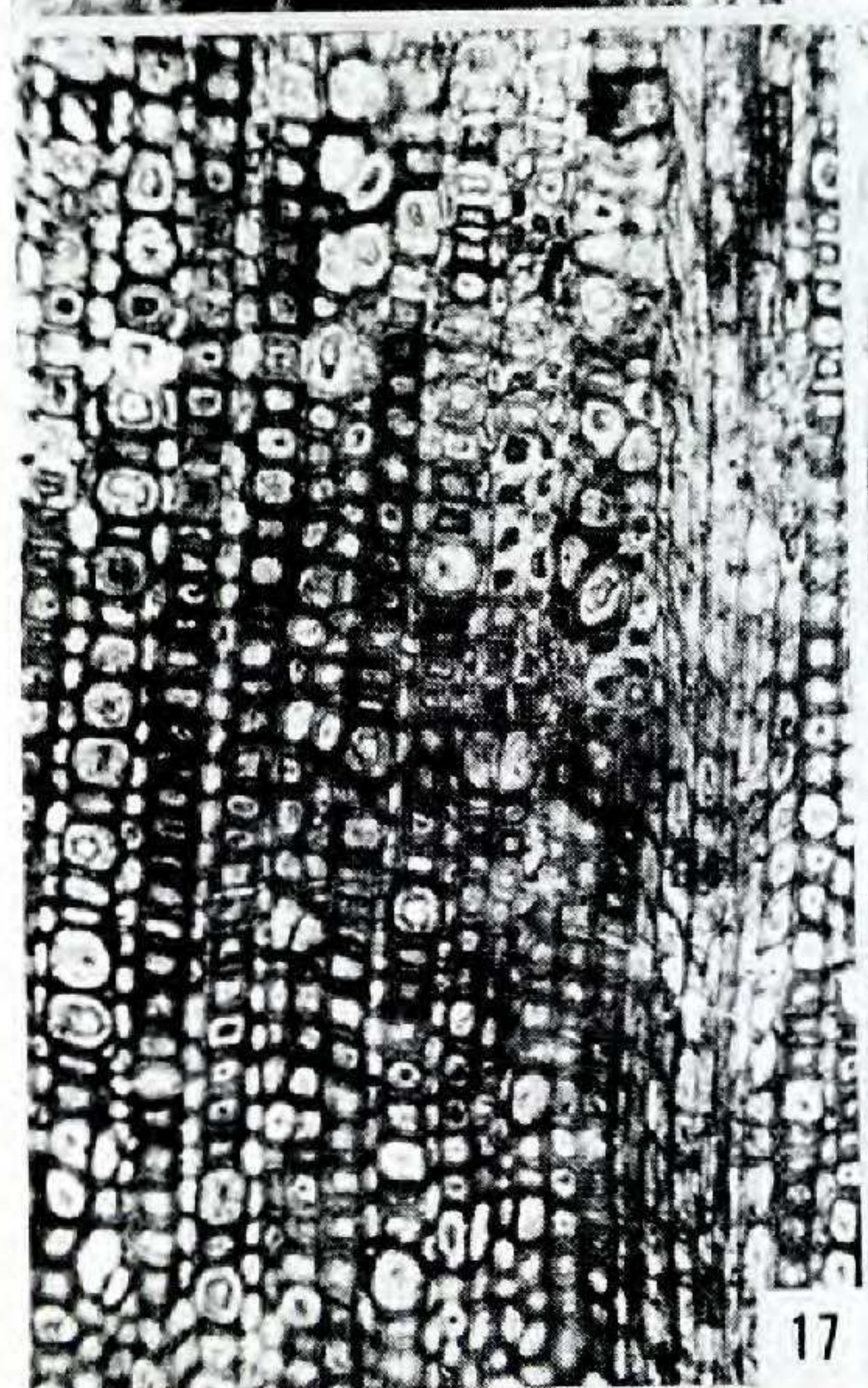
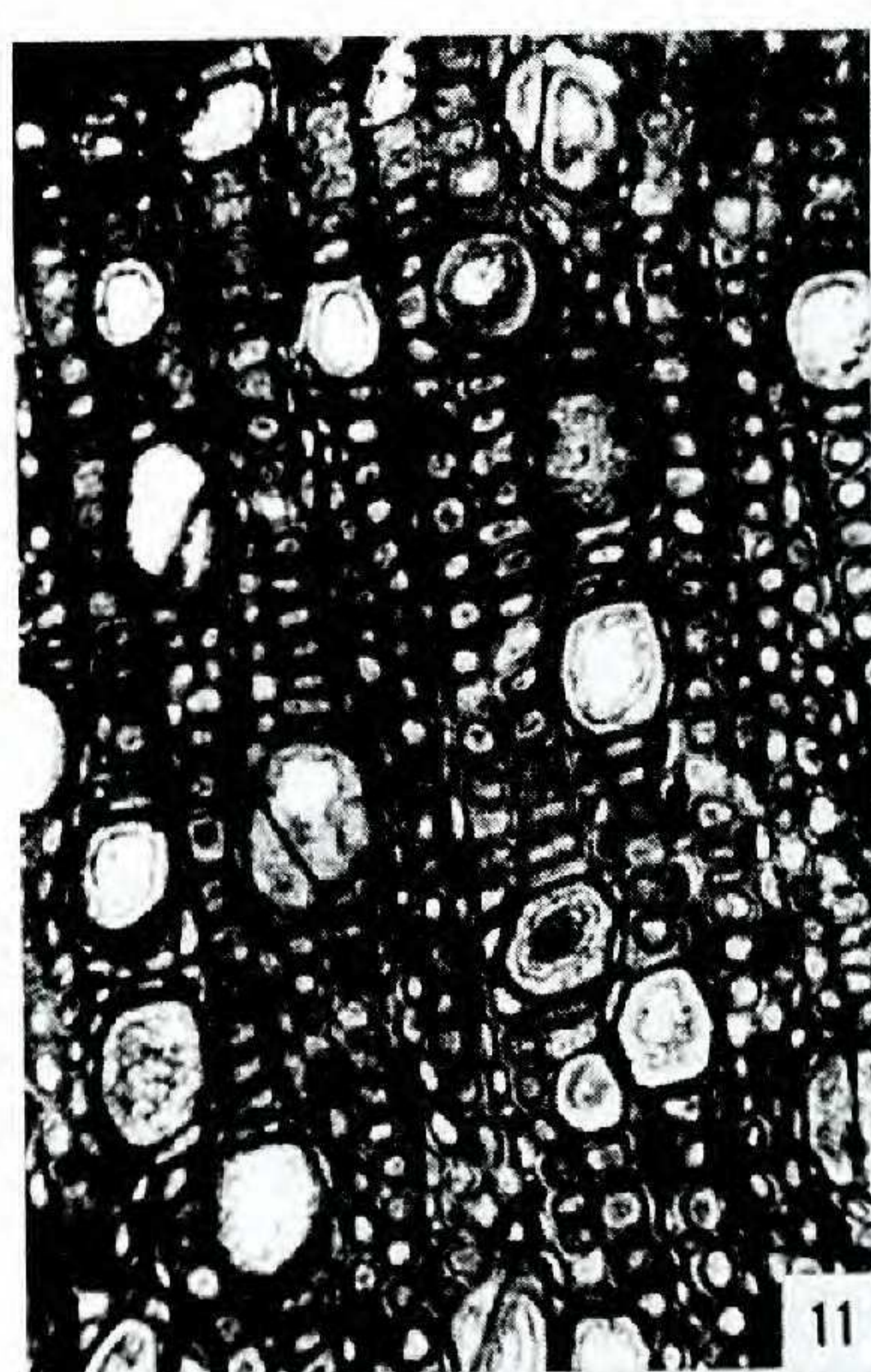
CASG 60120

FIGURES 17–20.

MATERIAL. Stem 3 cm. in diameter. Some primary xylem present.

Secondary xylem. Growth rings indistinct. Pores small, scarcely larger than fibers in transverse section, squarish, average radial diameter 33 μm . (29–39), average tangential diameter 32 μm . (26–37). Perforation plates scalariform, bars average 58 (20 to 70). Intervessel pits scalariform-transitional, grading into alternate in some; pits to ray cells similar, some small, round, and alternate; length of vessel elements about 600–800 μm . Parenchyma seems to be absent. Rays heterocellular, 2 to 4 cells wide, highly disorganized, cells in center of ray square or short procumbent, uniseriate margins one cell high, the cells upright; uniseriates up to 9 cells

FIGURES 11–20. 11–13, CASG 60118: 11, transverse section, $\times 75$; 12, radial section, $\times 40$; 13, tangential section (note high multiseriate ray), $\times 50$. 14–16, CASG 60122: 14, transverse section, $\times 43$; 15, radial section, $\times 70$; 16, tangential section, $\times 75$. 17–20, CASG 60120: 17, transverse section, $\times 73$; 18, tangential section, $\times 60$; 19, radial section (note high upright cells of uniseriate rays), $\times 40$; 20, radial section showing square and upright cells of multiseriate ray (note fiber septae in upper right), $\times 40$.



high, the cells high, upright; most ray cells contain a dark, amorphous substance. Many fibers septate.

LOCALITY. Unnamed site, locality 2b.

Cells of the uniseriate rays and of the uniseriate margins of the multiseriate rays are so high that they are difficult to distinguish from parenchyma cells. The absence of parenchyma is, therefore, not certain. Septate fibers, however, usually do not occur in wood with much apotracheal parenchyma. Perforation plates are at such an acute angle and are so long that it is possible to mistake bars of the plates for intervessel pits. The general pattern is similar to that of some species of *Illicium*, but, although septate fibers have been reported in one species by Kanehira (1921), they have not been observed in the species examined by me or by Metcalfe and Chalk (1950). There is a similarity to the wood of *Matthaea* of the Monimiaceae. Septate fibers are present in this genus, but the rays are very high. Vessel elements in the fossil are much shorter than those reported for mature wood of either *Illicium* or *Matthaea*. The length of these elements in immature wood is not known to me. Pollen similar to that of *Illicium* has been reported from locality 1 (Chmura, 1973).

CASG 60117

FIGURES 3, 5-7.

MATERIAL. Small stem 3 cm. in diameter. Growth rings visible with magnification; diffuse porous.

Secondary xylem. Pores solitary, small, more or less square, average radial diameter 58 μm . (35-70), average tangential diameter 52 μm . (29-57). Perforation plates scalariform, 50 to 100 closely spaced bars. Intervessel pits scarce, some appear to be scalariform; pits to ray cells small, opposite, some elongated horizontally; average length of vessel elements 1287 μm . (870-1824). Parenchyma diffuse, moderately abundant, some cells associated with vessels. Rays uniseriate, 40 to 60 cells high, cells mostly square and short procumbent.

Pith. Small; cells small, cuboidal.

Phloem. Rays uniseriate, not as frequent as in xylem. Cells become laterally extended in outer portion, walls become thickened. Groups of stone cells in outer layers. Fibers thick walled.

LOCALITY. Del Puerto Creek, locality 1.

The size and shape of the pith varies among different sections from more or less lobed to round. The former probably represents a nodal region, the latter an internode. The departure of portions of several branch traces can be observed in longitudinal section. The nature of the departure from the pith indicates an alternate branching system. High multiseriate rays occur in restricted areas in some tangential sections (FIGURE 7). These are probably branch traces. A radial section through the pith shows two

traces departing within a very short distance (2 mm.) of one another. In tangential section the traces are confined to a narrow portion. I assume that this represents a type of phyllotaxy in which the leaves are in close approximation vertically but not necessarily radially. Of the plants I have examined, those with crowded branches have small leaves.

Poor preservation obscured wall pits in most cells. It is not uncommon for solitary vessels to be devoid of pits except where the walls are in contact with parenchyma or where ends of elements in vertical file overlap. In several areas pits in the walls of ray cells are clearly visible, but in others it is difficult to determine whether the pits are on the ray cells or on walls of vessels. In addition, the excessively long perforation plates can be mistaken for scalariform wall pits where only a portion can be seen in radial section. Some vessels contain an amber-colored substance. There is some evidence of crystals in the phloem. Occasional parenchyma cells appear to have divided transversely, resulting in a vertical series of four small cells, each of which contains a small druse. Such crystals were not observed in other cell types.

The general features of the secondary xylem, to the extent that they can be observed, occur in *Clethra*, *Nyssa*, and certain genera of the Theaceae.

CASG 60118

FIGURES 11-13.

MATERIAL. Small stem 2.5 cm. in diameter. No growth rings apparent.

Secondary xylem. Pores solitary with some tendency to form multiples, overlapping pairs tangential, average radial diameter 68 μm . (46-87), average tangential diameter 59 μm . (40-80). Perforation plates scalariform, 50 to 100 fine bars, anastomoses frequent. Vessel pits scalariform-transitional; pits to ray cells and axial parenchyma similar; vessel elements average 1108 μm . (870-1334) in length; tyloses frequent. Parenchyma diffuse, not abundant. Rays high, multiseriate 4 to 8 cells wide, cells square and upright; uniseriate numerous, very high, cells upright. Fiber pits bordered, numerous in uniseriate vertical files, apertures included.

Pith. Round; numerous primary xylem points flanked by multiseriate rays; cells small, round, vertically elongated.

Phloem. Multiseriate rays of xylem continue into secondary phloem where they flare out as a result of lateral expansion of cells. Uniseriate also extend into phloem and together with thin-walled cells and fibers form wedges alternating with inverted wedges of expanded multiseriate rays. Each wedge of conducting cells and uniseriate rays capped by a small group of fibers.

LOCALITY. Black Gulch, locality 2a.

Similar wood patterns can be found in such families as the Nyssaceae, Theaceae, Icacinaceae (*Platea*), and Aquifoliaceae (*Phelline*).

CASG 60119

FIGURES 8–10.

MATERIAL. Small stem 3.5 cm. in diameter. Growth rings faint.

Secondary xylem. Pores mostly solitary with some tangentially aligned in clusters of 2 to 4, angular, average radial diameter 104 μm . (81–110), average tangential diameter 80 μm . (69–92). Perforation plates scalariform, bars average 53 (47 to 65), some reticulate. Intervessel pits small, transitional-opposite; pits to ray cells similar; vessel elements average 1156 μm . (980–1276) in length; tyloses thin walled. Parenchyma abundant, diffuse. Rays numerous, each vessel flanked by a ray of some kind; multiseriates high, some vertically joined and some dissected, mostly 4 to 5 cells wide, the cells square, upright, and short procumbent, sheath cells common; uniseriate margins up to 14 cells high, cells upright; uniseriates up to 14 cells high, cells square and upright. Fiber pits numerous, small, bordered, on all walls, apertures included.

Pith. Round; primary xylem points numerous; cells large, flattened in long section, arranged in vertical rows.

LOCALITY. Black Gulch, locality 2a.

Group IIB woods with vessel elements over 1 mm. in length and small intervessel and vessel-ray pits are: Nyssaceae, Clethraceae, and some Theaceae.

CASG 60130

FIGURES 24–27.

MATERIAL. Portion of a small branch 1.5 cm. from the pith through the phloem, which is 2 mm. thick at its widest.

Secondary xylem. Pores solitary, small, squarish, average radial diameter 46 μm . (40–58), average tangential diameter 45 μm . (40–52). Perforation plates scalariform, average 54 (25 to 99) closely spaced bars. Intervessel pits opposite-transitional, scalariform and bordered in ligules of some, occasionally on entire wall; pits to rays similar; pits to parenchyma scalariform; average vessel element length 1008 μm . (782–1132). Parenchyma abundant, diffuse, some in tangential uniseriate rows, many cells high, contents brown. Rays up to 12 cells wide, 5–7 mm. high, cells square and upright, uniseriate margins lacking; uniseriates of narrow, upright cells in tangential view, numerous, up to 12 cells high; multiseriates frequent, more or less equidistant, narrow at pith becoming wider in later increments, some dissected. Fibers thick walled, the pits small, bordered, on all walls.

Pith. Small; cells small at periphery and larger at center, rectangular in long section. Medullary rays separate protoxylem points.

Phloem. All rays continue into phloem; broad rays dip into xylem at cambium junction and flare out slightly in outer layers of phloem; walls



FIGURES 21-29. 21-23, CASG 60129: 21, transverse section, $\times 60$; 22, radial section, $\times 60$; 23, tangential section, $\times 40$. 24-27, CASG 60130: 24, transverse section, $\times 65$; 25, transverse section showing phloem (note regular spacing of multiseriate rays), $\times 30$; 26, radial section, $\times 65$; 27, tangential section, $\times 65$. 28, 29, CASG 60131: 28, radial section, $\times 60$; 29, tangential section, $\times 60$.

of fibers thick, lumen almost obliterated in some; rhomboidal crystals in some parenchyma cells.

LOCALITY. Black Gulch, locality 2a.

Except for the subfamily Dilleniaceae of the Dilleniaceae, Group II woods with similar patterns have vessel elements shorter than 900 μm . (Cyrillaceae, Icacinaceae, Eupteleaceae).

The following 11 specimens (CASG 60122, CASG 60127, CASG 60208, CASG 60124, CASG 60126, CASG 60125, CASG 60128, CASG 60129, CASG 60131, CASG 60132, and CASG 60134) are classified in Group IIIB section 2. Some extant genera in this group with vessel elements longer than 900 μm . are members of the Dilleniaceae, Theaceae, Symplocaceae, Nyssaceae, Euphorbiaceae (*Protomegabaria*), Daphniphyllaceae, Buxaceae, and Cornaceae. Genera of this category with vessel elements shorter than 900 μm . belong to the Theaceae, Cunoniaceae, Cornaceae, Icacinaceae, Buxaceae, Ericaceae, Escalloniaceae, and Hamamelidaceae.

The first seven specimens are closely similar but differ in a few details. While some of these differences are the kinds that can be observed between roots and stems or between early- and later-formed wood of the same plant, others may reflect taxonomic disparities of a high order. The pattern is represented in all three localities. Because of the close similarity, only the first specimen is illustrated.

CASG 60122

FIGURES 14–16.

MATERIAL. Secondary wood 2.5 cm. in diameter in transverse section. The angle of divergence of the rays suggests that the fragment may have been near the pith. Growth rings are not evident.

Secondary xylem. Pores solitary, angular, with a slight tendency to radial alignment, average radial diameter 100 μm . (64–128), average tangential diameter 80 μm . (58–99). Perforation plates scalariform, bars average 17 (10 to 30); average length of vessel elements 1171 μm . (986–1232); intervessel pits opposite, transitional in vicinity of perforation plates, very small; pits on tangential walls few, scattered; pits to ray cells small, numerous. Parenchyma not abundant, mostly apotracheal diffuse. Rays 3 or 4 cells wide, heterocellular, some vertically joined by uniseriate margins composed of upright cells; cross walls of upright cells oblique, sheath cells common; uniseriates 1 to 4 cells high, cells upright. Fiber pits small, numerous, apertures included.

LOCALITY. Del Puerto Creek, locality 1.

CASG 60127

MATERIAL. Fragment of mature secondary xylem 4 cm. by 2.5 cm. in transverse section. Growth rings not evident.

Secondary xylem. Pores large, solitary, average radial diameter 142 μm . (58–203), average tangential diameter 93 μm . (58–133). Perforation plates scalariform, 30 to 50 bars. Length of vessel elements average 2024 μm . (1400–2436). Parenchyma abundant, apotracheal diffuse. Rays heterocellular with high uniseriate margins, multiseriate portion of low procumbent cells, 3 or 4 cells wide, many joined vertically by uniseriate margins; uniseriates 14 or more cells high, cells upright.

LOCALITY. Del Puerto Creek, locality 1.

CASG 60208

MATERIAL. Small stem 1 cm. in diameter with large pith and only a small amount of secondary xylem.

Secondary xylem. Pores mostly solitary, diffuse, slightly angular, average radial diameter 97 μm . (58–116), average tangential diameter 71 μm . (58–87). Perforation plates scalariform, bars average 30 (up to 50), plates very oblique. Intervessel pits opposite-transitional; average vessel element length 655 μm . (580–754). Parenchyma abundant, apotracheal diffuse. Rays 1 to 6 cells wide, very high, cells square and upright. Fibers thick walled, pits bordered.

Pith. Large; with many protoxylem points and large, saclike cavities lacking epithelium. Sacs slightly elongated vertically with no interconnection or contents. The sacs could be interpreted as lysigenous, rhexigenous, or the result of postmortem microbial activity.

LOCALITY. Del Puerto Creek, locality 1.

CASG 60124

MATERIAL. A fragment of secondary xylem 1.5 cm. by 2 cm. in transverse section. Secondary walls absent in most cells. Growth rings not observed.

Secondary xylem. Pores solitary, large, average radial diameter 102 μm . (86–128), average tangential diameter 82 μm . (72–100). Perforation plates scalariform, 25 to 30 bars. Intervessel pits large, opposite; pits to ray cells similar or laterally elongated; pits to axial parenchyma round; average length of vessel elements 1062 μm . (858–1187). Parenchyma apotracheal diffuse, abundant. Rays heterocellular, 3 or 4 cells wide, numerous, uniseriate margins mostly 1 to 3 cells high, cells upright; cells of multiseriate portion square or procumbent, sheath cells common. Fibers with bordered pits, apertures included.

LOCALITY. Black Gulch, locality 2a.

CASG 60126

MATERIAL. Stem or root 5 cm. in diameter. Growth rings absent.

Secondary xylem. Pores large, oval, solitary, average radial diameter 157 μm . (114–200), average tangential diameter 89 μm . (78–143). Perforation plates scalariform, 30 to 40 bars. Average length of vessel elements 1624 μm . (1276–1850); tyloses. Parenchyma abundant, apotracheal diffuse. Rays heterocellular, up to 5 cells wide, with high uniseriate margins, cells square and upright, some connected by uniseriate margins; uniseriates up to 20 cells high, cells upright. Rhomboidal crystals occasional.

LOCALITY. Black Gulch, locality 2a.

CASG 60125

MATERIAL. Secondary xylem 1.5 cm. by 3 cm. in transverse section. Curvature of the periphery of the section coincides with demarcation of growth increment and indicates outer edge was about 2 cm. from center of axis. Growth rings indistinct.

Secondary xylem. Pores mostly solitary with some clusters of 3, average radial diameter 147 μm . (70–203), average tangential diameter 118 μm . (75–158). Perforation plates scalariform, bars average 30 (18 to 70), very oblique. Intervessel pits opposite, transitional in smaller vessels; pits to ray cells small, numerous; average length of vessel elements 1507 μm . (986–2030); tyloses. Parenchyma abundant, apotracheal diffuse. Rays heterocellular, high, many vertically joined by uniseriate margins; margins 4 to 8 cells high, sheath cells in some; uniseriates up to 20 cells high, cells upright; rhomboidal crystals occasional. Fibers with numerous bordered pits.

LOCALITY. Black Gulch, locality 2a.

CASG 60128

MATERIAL. Stem 5 cm. in diameter. Growth rings absent.

Secondary xylem. Pores solitary, large, angular, average radial diameter 114 μm . (87–145), average tangential diameter 75 μm . (70–104). Perforation plates scalariform, bars average 25 (16 to 40). Intervessel pits scarce, opposite to transitional in ligules; pits to ray cells scalariform; pits to parenchyma small; average length of vessel elements 928 μm . (580–1160); tyloses abundant. Parenchyma abundant, apotracheal diffuse, cells with dark contents. Rays heterocellular, 2 to 4 cells wide; multiseriate portion in tangential view scarcely wider than uniseriate margins, many connected vertically by margins; margins several cells high, the cells upright, square, or short procumbent; uniseriates 3 to 16 cells high, cells upright; rays variable in height, true uniseriates infrequent. All cells with dark contents. Fibers with bordered pits, apertures included, contents dark colored.

LOCALITY. Unnamed site, locality 2b.

The only specimens of this group that contain crystals are CASG 60125 and CASG 60126, collected from locality 2a. They are closely similar to CASG 60128, from locality 2b, but in this specimen the imperforate elements contain dark, amorphous inclusions. CASG 60124 (locality 2a) lacks both crystals and dark inclusions, but like CASG 60128 it has large vessel-ray pits, while in CASG 60125 they are small (none was observed in CASG 60126). In locality 1, two extremes in length of vessel elements occur: the shortest (avg. 655 μm .) in CASG 60208, a young stem; the longest (avg. 2024 μm .) in CASG 60127, mature wood. Moreover, perforation plates in CASG 60122 (also from locality 1) have the lowest number of bars (as well as the least amount of parenchyma) of any specimen among the seven. It is not unlikely that CASG 60208 and CASG 60127 represent different stages of stem development in the same species, while CASG 60122 is unrelated. Specimen CASG 60119 (locality 2a), described earlier, is similar to CASG 60124, but the perforation plates have many more bars.

Although these specimens are closely similar in general structure, we may be dealing with more than one taxon at the level of genus or higher. This interpretation is reinforced by circumstances under which the specimens were deposited. As will be discussed later, the estimated time span of the three localities is over a million years, or a period that may have encompassed several cycles of climatic—and hence vegetational—change. Furthermore, the basic structural pattern with the variations observed in the fossils occurs in a cluster of modern families, most notably the Dilleniaceae, Theaceae, Symplocaceae, Nyssaceae, Cornaceae, Euphorbiaceae, Daphniphyllaceae, and Buxaceae. Pollen attributable to the Symplocaceae, Nyssaceae, Cornaceae, and Buxaceae (*Sarcandra*, *Pachysandra*) has been reported from localities 1 and 2a (Chmura, 1973).

CASG 60129

FIGURES 21–23.

MATERIAL. A wedge of secondary xylem from a small stem or root originally at least 4 cm. in diameter. The transverse view indicates that the specimen was close to the center of the axis. Growth rings absent.

Secondary xylem. Pores solitary, oval, average radial diameter 122 μm . (87–145), average tangential diameter 75 μm . (58–87). Perforation plates scalariform, bars average 40 (30 to 60). Intervessel pits opposite, small; pits to ray cells similar; average vessel element length 765 μm . (580–986). Parenchyma abundant, apotracheal diffuse. Multiseriate portion of rays 3 cells wide, cells mostly procumbent; height of uniseriate margins variable, 1 to several cells, cells square and upright; uniseriates 2 to 10 cells high, cells upright.

LOCALITY. Del Puerto Creek, locality 1.

Uniseriate rays are abundant in transverse section near what was probably the primary xylem. Multiseriates begin at various distances from this part of the section and increase in number toward the outer edge. Changes in structure are also reflected in the presence of lower multi-

seriates with fewer rows of marginal cells in the outer portion. The mature rays may have been of this type. The wood pattern is common to several families. Examples are species of *Cornus* (Cornaceae), *Leplacea* (Theaceae), and *Weinmannia* (Cunoniaceae).

CASG 60131

FIGURES 28–31.

MATERIAL. Fork of branching axis originally at least 3 cm. in diameter.

Secondary xylem. Pores mostly solitary, some groups of 2 or 3, average radial diameter 75 μm . (46–87), average tangential diameter 69 μm . (52–87). Perforation plates scalariform, up to 30 bars. Intervessel pits opposite and, at least near ends of elements, occasionally scalariform, mostly small, round; pits to ray cells horizontally elongated; average vessel element length 754 μm . (580–812); tyloses common, thin walled. Parenchyma apotracheal diffuse. Multiseriate rays mostly 5 or 6 cells wide, the cells thick walled, mostly square and short procumbent with usually one marginal row of square cells, some rays narrow with several rows of marginal upright cells; uniseriates low, 2 to 5 upright cells. Fibers thick walled, the pits slitlike, small, bordered. All cells contain dark, amorphous inclusions.

Pith. Small, squarish; with plates of sclereids. Medullary rays extend into xylem as multiseriates.

LOCALITY. Black Gulch, locality 2a.

Among genera of Group IIIB section 2 with vessel elements less than 900 μm . long, the Cunoniaceae and related Eucryphiaceae are reported to have a quadrangular pith. Dark, amorphous inclusions occur in the imperforate elements in both families.

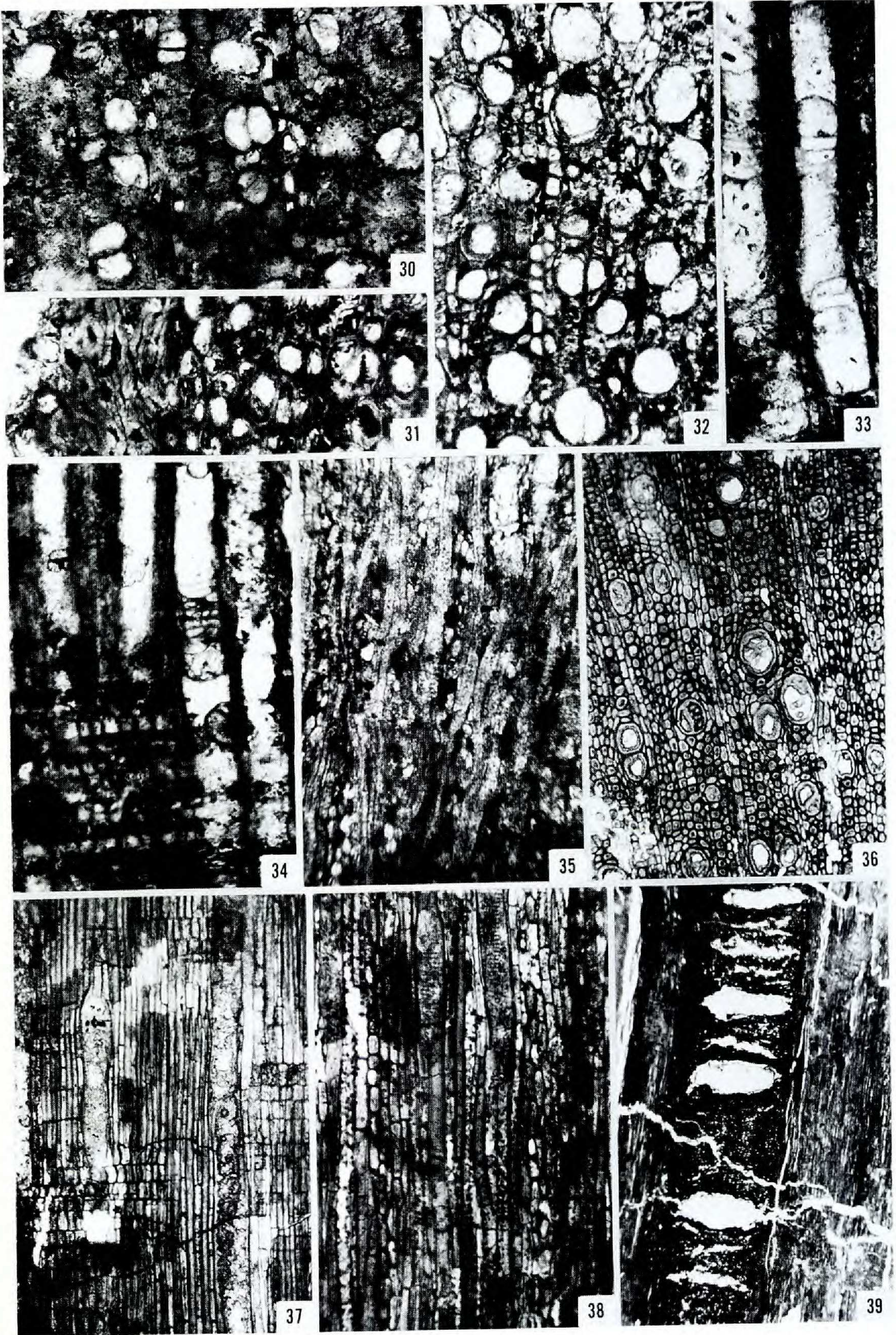
CASG 60132

FIGURES 36–39.

MATERIAL. Small stem 2 cm. in diameter. Growth rings absent.

Secondary xylem. Pores mostly solitary, angular with some radial groups of three, average radial diameter 172 μm . (87–185), average tangential diameter 87 μm . (64–127). Perforation plates scalariform, bars average 20 (10 to 29). Intervessel pits very small, numerous, opposite; pits to ray cells similar; pits in axial parenchyma numerous, small to elongated horizontally; average length of vessel elements 838 μm . (580–986). Parenchyma abundant, apotracheal diffuse. Multiseriate rays up to 15

FIGURES 30–39. 30, 31, CASG 60131: 30, transverse section, $\times 60$; 31, longitudinal section of pith showing sclereids, $\times 60$. 32–35, CASG 60134: 32, transverse section, $\times 75$; 33, scalariform perforation plates, $\times 75$; 34, radial section, $\times 75$; 35, tangential section, $\times 60$. 36–39, CASG 60132: 36, transverse section, $\times 40$; 37, radial section (note abundant axial parenchyma), $\times 40$; 38, tangential section, $\times 40$; 39, longitudinal section of pith showing lacunae, $\times 4$.



cells wide, very high, cells mostly square or upright; uniseriates 3 to 10 cells high, cells upright. Chambered crystals in some upright cells. Fiber pits small, bordered.

Pith. Many primary xylem points separated by medullary portion of wide rays. Cells in center large, smaller at periphery.

LOCALITY. Del Puerto Creek, locality 1.

In longitudinal section the pith appears to be chambered (FIGURE 39), but the lacunae are at irregular intervals and appear to have resulted from mechanical rupture of the tissue. The wood pattern falls within the range of variation of Bailey and Howard's (1941) Group I Icacinaceae. Single rhomboidal crystals have been observed in individual ray cells in this group, but chambered crystals have not been reported. Intervessel pits in this group are not particularly small.

CASG 60134

FIGURES 32–35.

MATERIAL. Stem 2.5 cm. in diameter including a large pith.

Secondary xylem. Pores solitary, numerous, average radial diameter 73 μm . (64–77), average tangential diameter 58 μm . (58–64). Perforation plates scalariform, less than 10 (mostly 4 or 5) widely spaced bars. Intervessel pits opposite to almost alternate, some laterally elongated; pits to ray cells large, laterally elongated; average length of vessel elements 476 μm . (3 measurements only); thin-walled tyloses common. Parenchyma apotracheal diffuse. Multiseriate rays 2 or 3 cells wide, cells square and short procumbent. Fibers thick walled, the pits numerous, large, flattened.

Pith. Over 1 cm. in diameter; cells near primary xylem thick walled, those in interior thin walled.

LOCALITY. Black Gulch, locality 2a.

Proper tangential sections were not obtained except near the pith. Convoluted, thick-walled, hyphaelike cells occupy a portion of the pith and can be confused with the thick-walled pith cells, although the latter possess pits, while the hyphaelike cells do not. Few families that have Group IIIB section 2 type wood, perforation plates with fewer than 10 bars, and vessel elements shorter than 600 μm . also have large vessel-ray pits. The Hamamelidaceae is one of those few.

The following three specimens (CASG 60135, CASG 60206, and CASG 60207) are classified as Group IIIB section 3. Woods of some extant genera of this group with vessel elements less than 900 μm . in length and with less than 15 bars in the perforation plates are members of the Caprifoliaceae, Garryaceae, Epacridaceae, and Ericaceae. Woods with an average of more than 15 bars occur in the Ericaceae and Icacinaceae.

CASG 60135

FIGURES 40–44.

MATERIAL. Small stem 2 cm. in diameter. Growth rings apparent with magnification.

Secondary xylem. Pores small, solitary, average radial diameter 69 μm . (58–87), average tangential diameter 60 μm . (52–70). Perforation plates scalariform, bars average 15 (10 to 25). Intervessel pits small, opposite to alternate; pits to ray cells small, numerous, apertures narrow; average vessel element length 661 μm . (580–754). Parenchyma abundant with tendency toward uniseriate tangential rows. Multiseriate rays 2 or 3 cells wide, cells square and procumbent; uniseriate margins of square and upright cells; uniseriates 3 to 5 cells high, cells upright. Fiber pits small, bordered, on all walls; tracheids occasional.

Pith. Oblong in transverse view.

Phloem. Cells mostly thin walled with staggered small patches of large stone cells. Rhomboidal crystals common in parenchyma.

LOCALITY. Unnamed site, locality 2b.

Pyrite obscures most of the cells in this specimen. Wall pits are preserved in many areas, but it is often difficult to determine whether they are parenchyma, ray, tracheid, or vessel pits. Pits that are definitely on intervessel walls are small and tend to be somewhat laterally elongated. There is a tendency to an alternate arrangement in some areas. Pits on the walls of fibers, ray cells, and what are interpreted as tracheids have oblique apertures (FIGURE 43).

The general pattern is similar to that of woods of species of the Ericaceae. Tracheidlike elements are occasionally associated with vessels in this family. The oblong pith in the fossil suggests that the plant had opposite leaves; in fact, one section shows two branch traces departing from opposite sides of the pith. Some Ericaceae have opposite phyllotaxy.

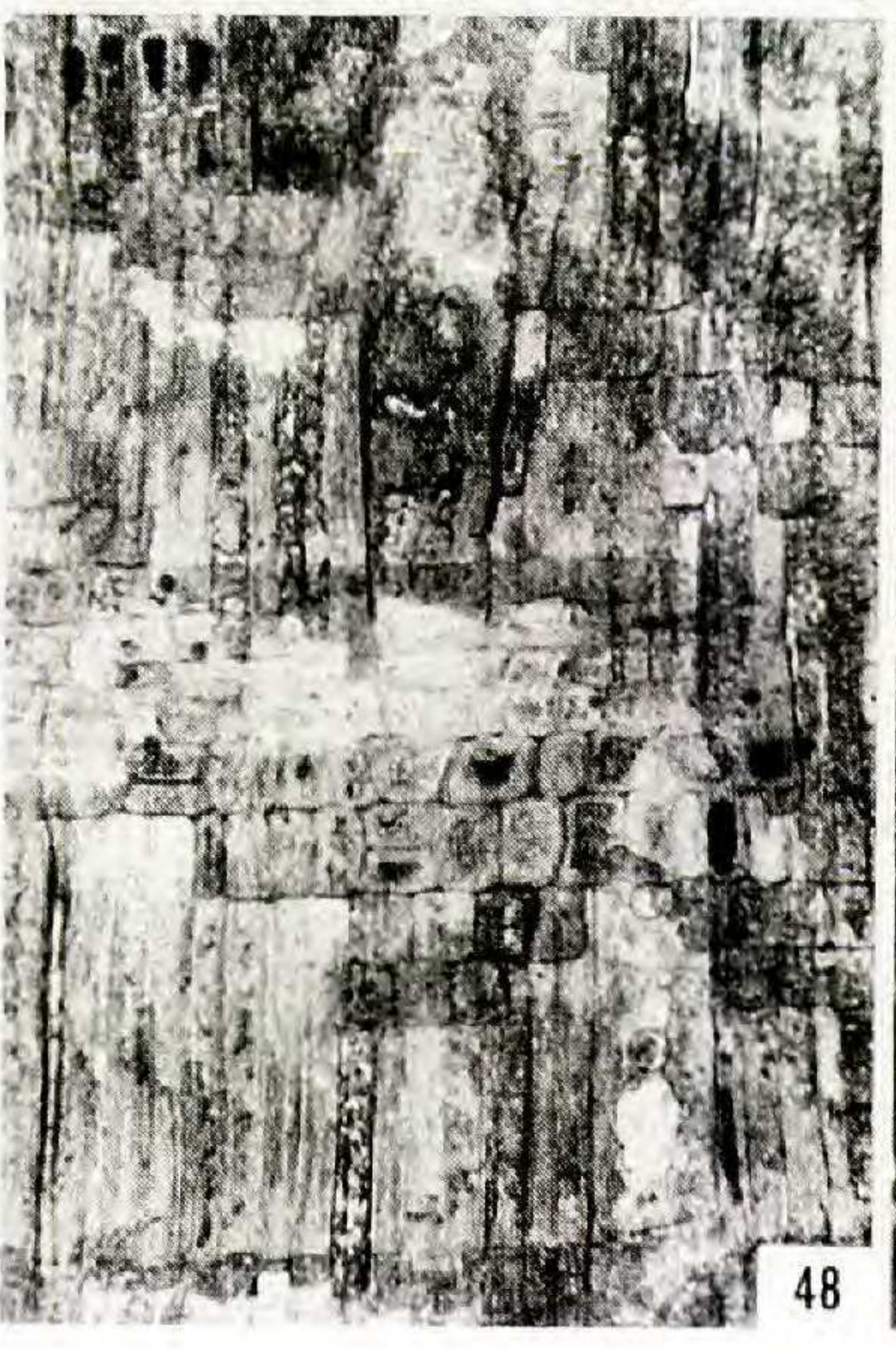
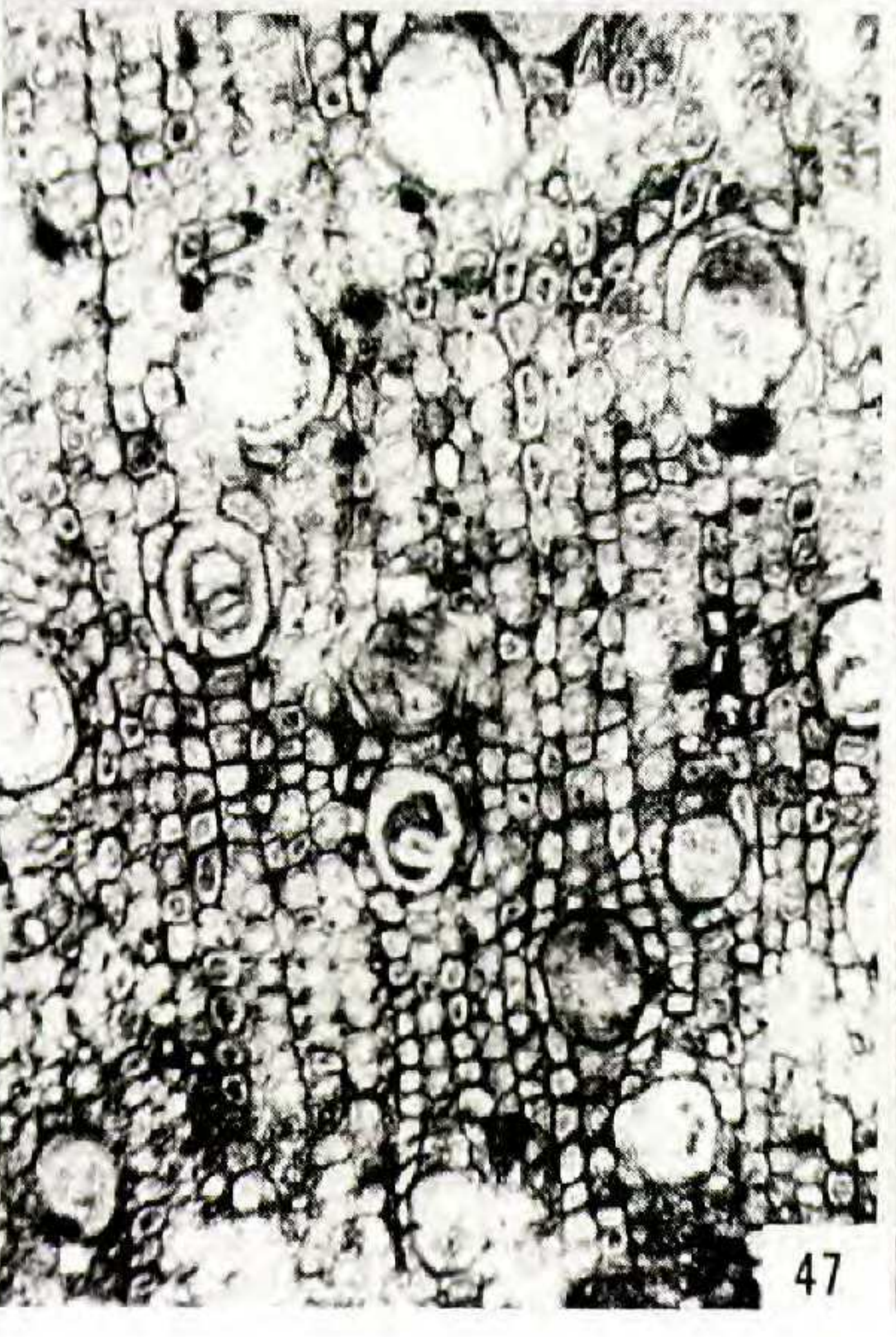
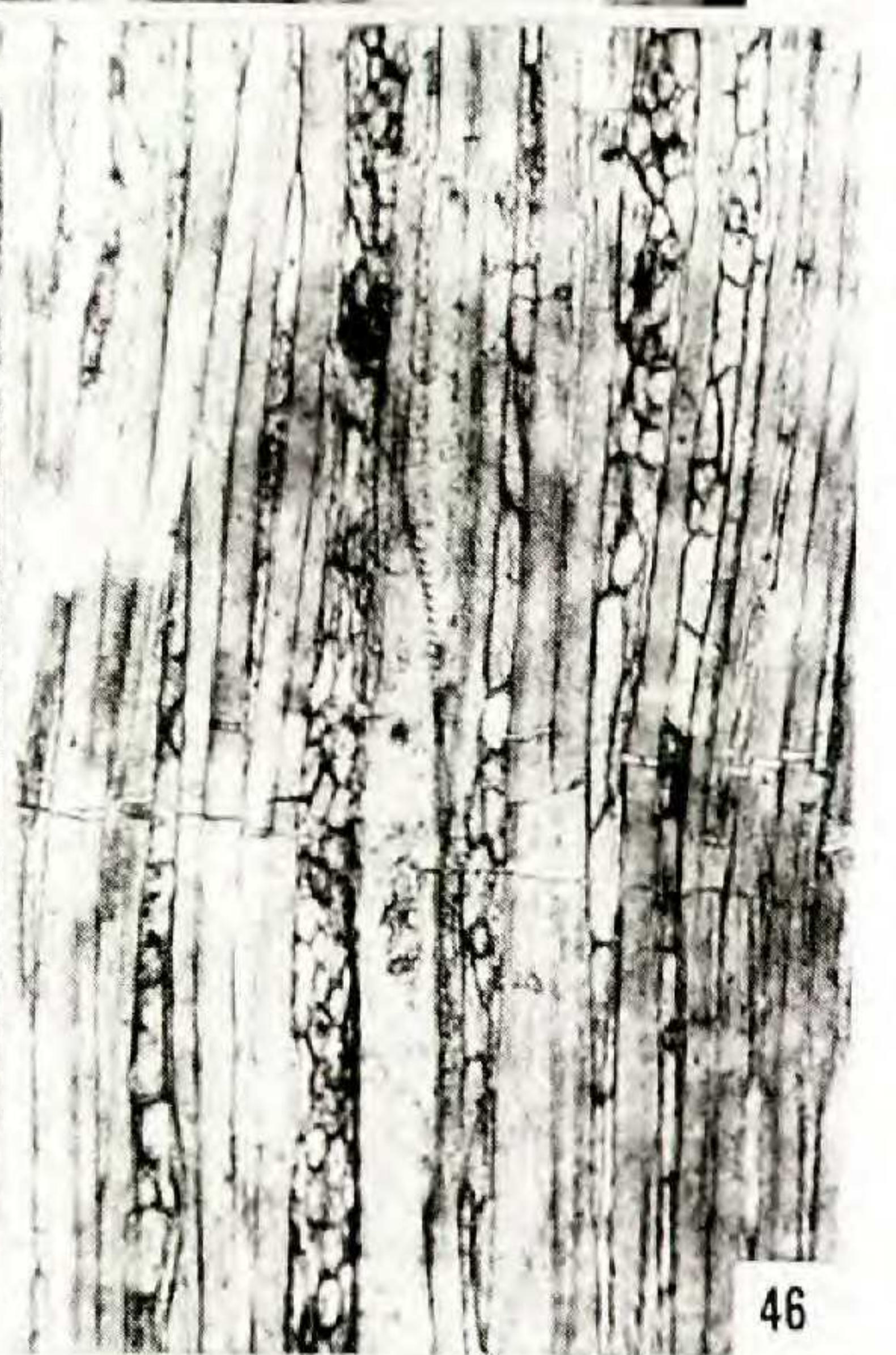
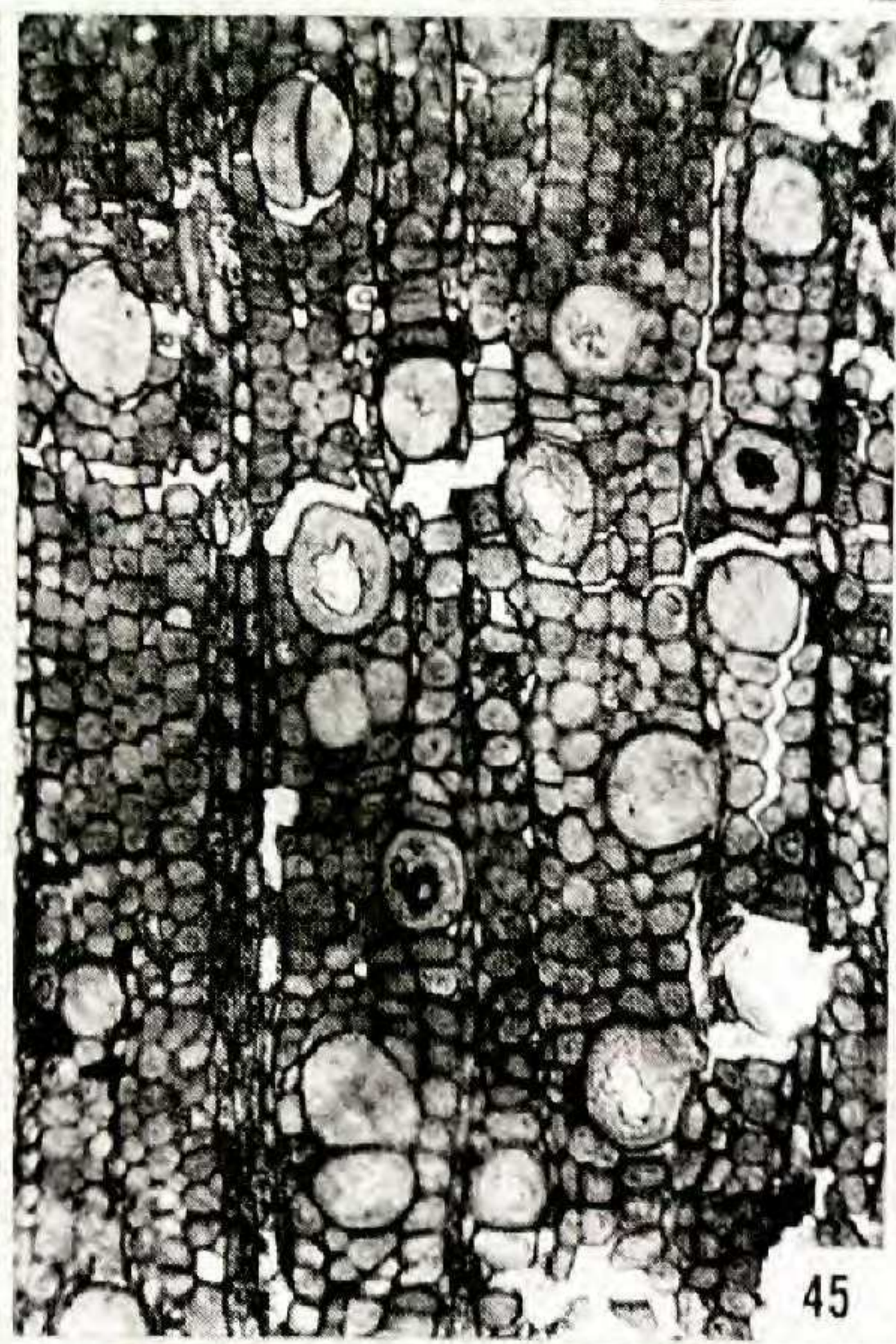
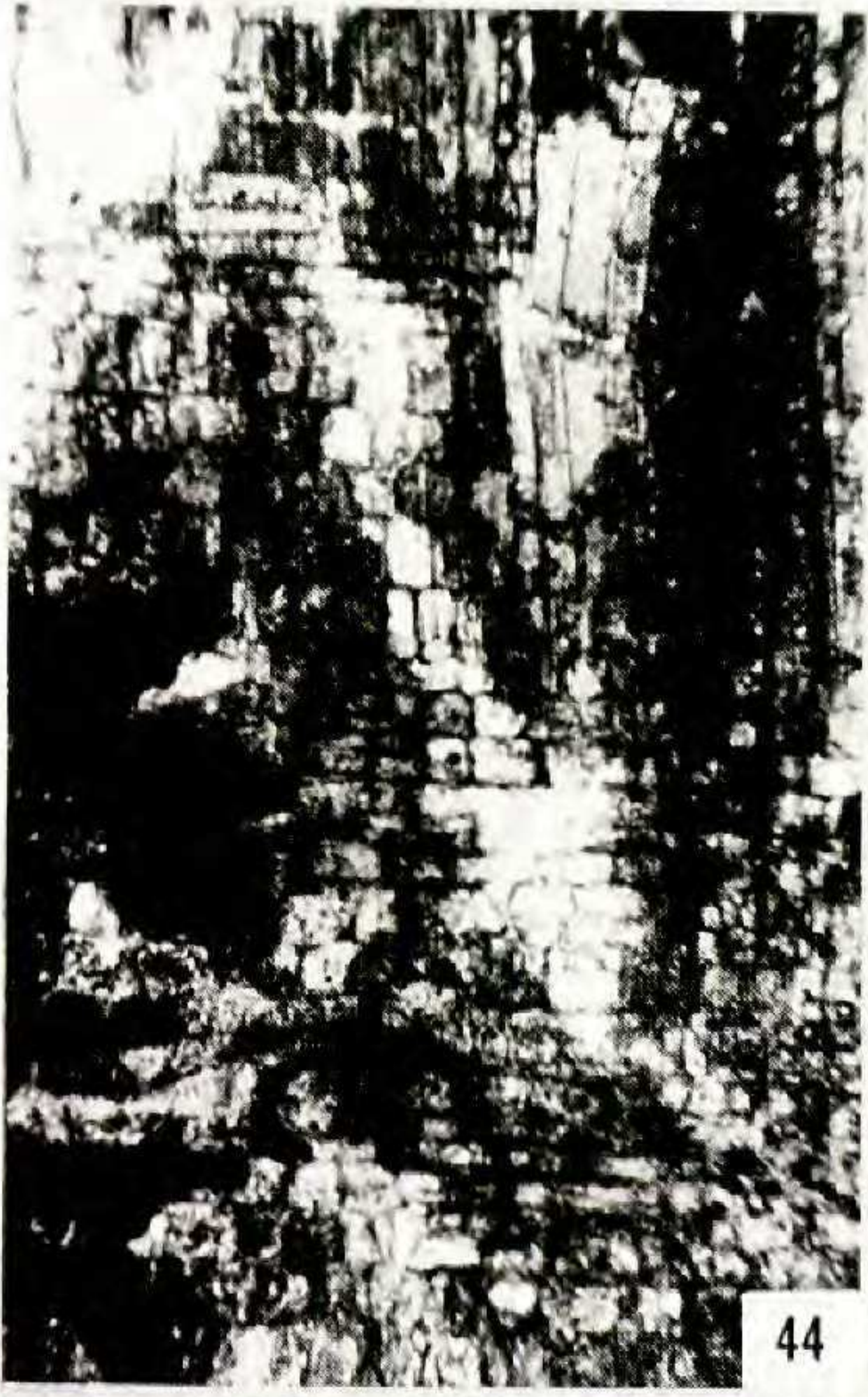
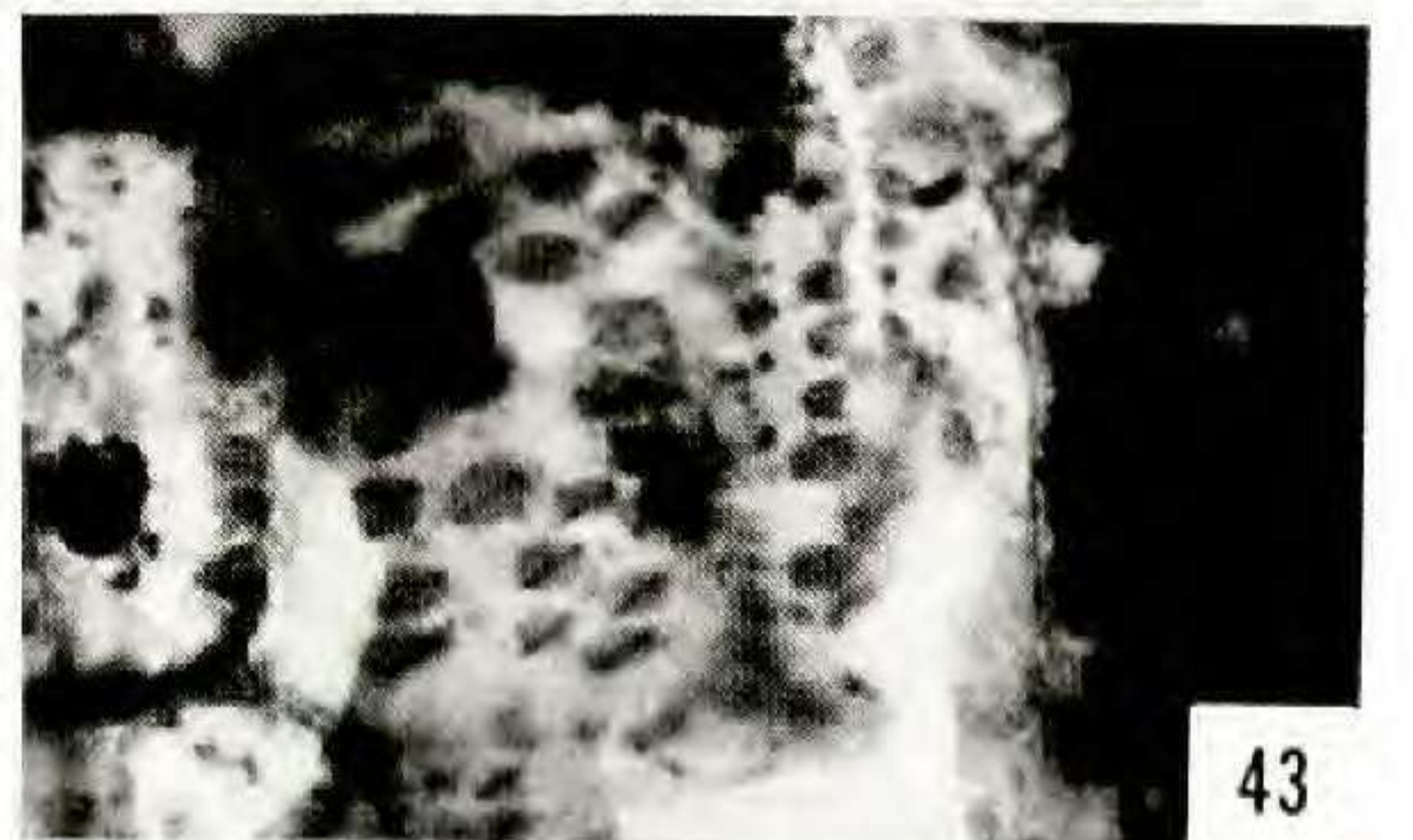
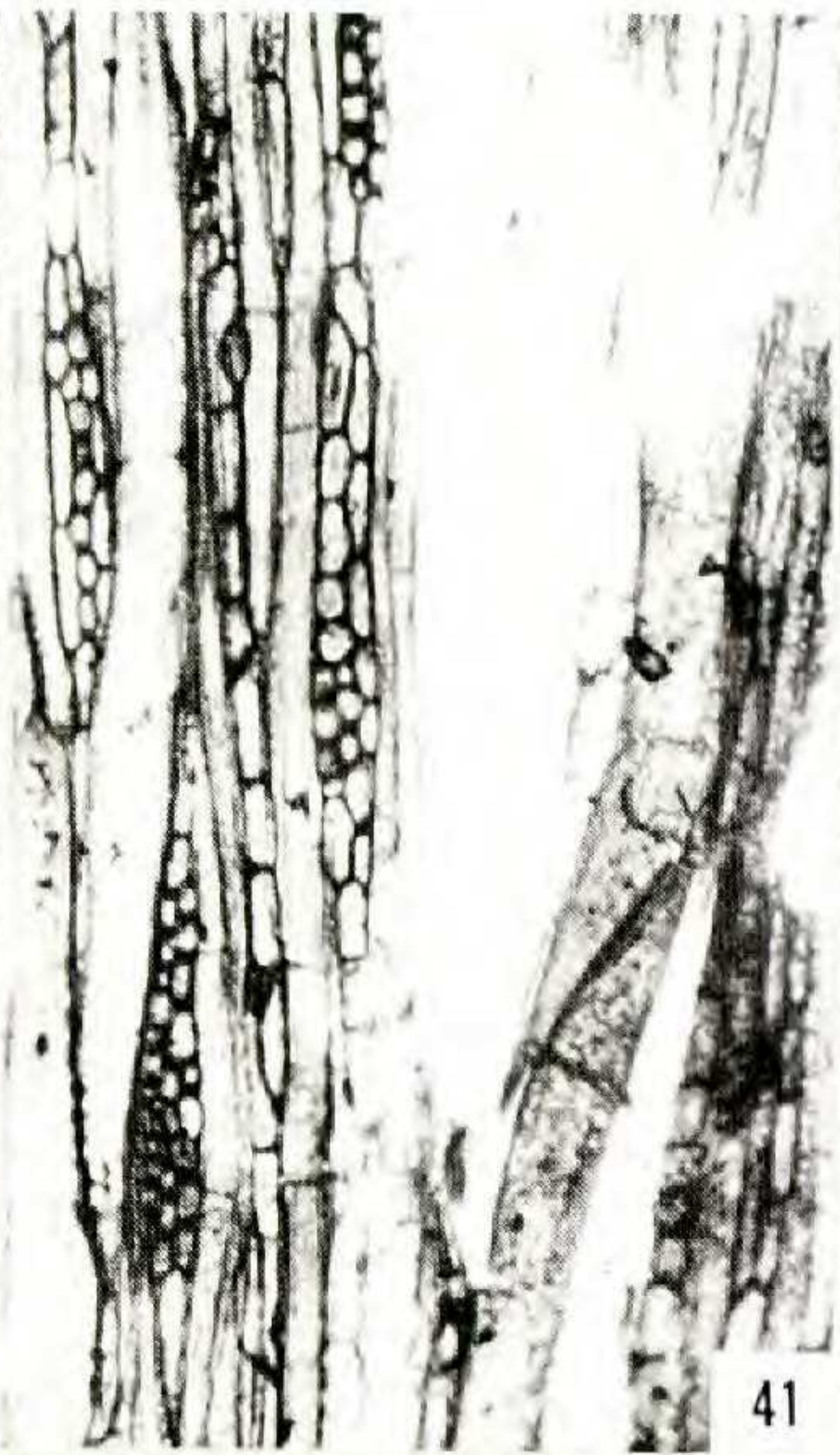
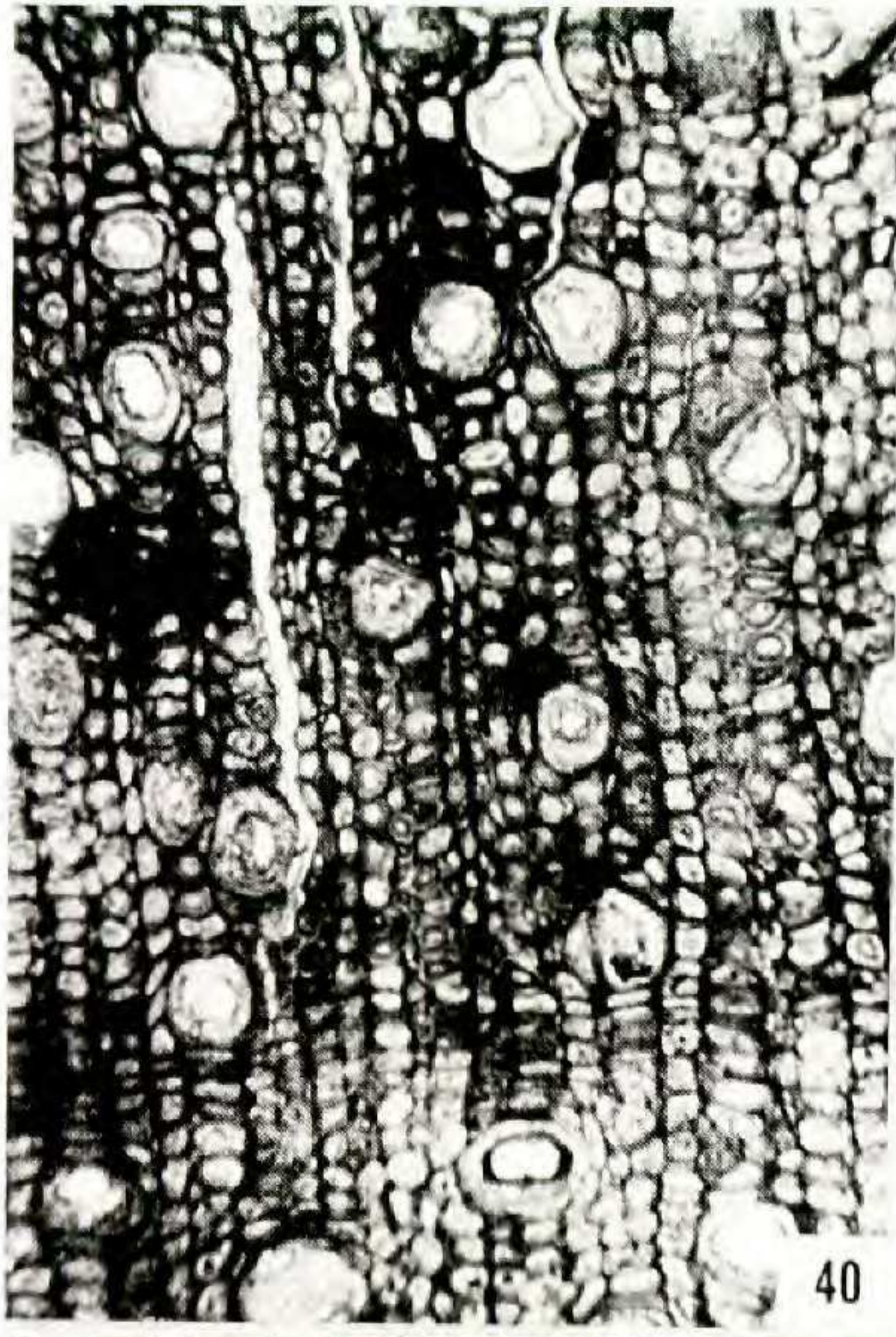
CASG 60206

FIGURES 45, 46.

MATERIAL. Stem 2.5 cm. in diameter.

Secondary xylem. Pores solitary, small, average radial diameter 53 μm . (36–71), average tangential diameter 48 μm . (36–57). Perforation plates scalariform with an average of 24 (20 to 40) coarse bars. Intervessel pits opposite to mostly alternate, numerous, small; pits to ray cells small, round; average length of vessel elements 608 μm . (580–928). Parenchyma apotracheal diffuse, abundant. Multiseriate rays 3 or 4 cells wide, cells variable in size and shape; uniseriate margins from one to many cells high, cells upright; uniseriates numerous, the cells high, upright. Fibers thick walled, the pits small, bordered.

Pith. Large; cells large.



Phloem. Sclereids arranged in irregular tangential lines.

LOCALITY. Del Puerto Creek, locality 1.

High, broad rays, prominent in one part of the tangential section, may be associated with a branch. Individual imperforate vascular elements occur within the rays. The wood pattern has some features in common with certain Cornaceae, Ericaceae, and Icacinaceae (*Apodytes*).

CASG 60207

FIGURES 47–49.

MATERIAL. Small stem with pith. Growth rings indistinct.

Secondary xylem. Pores mostly solitary with occasional clusters of 3, slightly angular to rounded, average radial diameter 74 μm . (57–94), average tangential diameter 58 μm . (50–64). Perforation plates scalariform, bars average 12 (4 to 38). Intervessel pits rare, opposite to alternate in ligules, laterally elongated and arranged in loose vertical files in some; pits to ray cells numerous, small, arrangement random; average vessel element length 657 μm . (626–1550). Parenchyma diffuse. Multiseriate rays 2 to 4 cells wide with high uniseriate margins of high upright cells, cells of multiseriate portion procumbent, many rays vertically joined by uniseriate margins; uniseriates 10 to 15 cells high, cells upright and square; rays near pith uniseriate, becoming biseriate and multiseriate in later-formed wood. Fibers thick walled with bordered pits on all walls.

Pith. Small; cells large and round in transverse section, flattened in long section. Primary xylem points separated from pith cells by groups of fibers.

LOCALITY. Black Gulch, locality 2a.

The wide range in length of vessel elements, as well as the differences between rays in early- and later-formed wood, indicates that the stem was in a transitional stage of maturation. This pattern could be typical of young stems of a number of Group IIIB families in which the vessel elements are longer than 1 mm. in the mature wood, such as the Cornaceae, Icacinaceae, and Caprifoliaceae.

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FIGURES 40–49. 40–44, CASG 60135: 40, transverse section, $\times 80$; 41, tangential section, $\times 80$; 42, transverse section of outer phloem (note patches of large stone cells), $\times 75$; 43, pits of ray cell, $\times 300$; 44, radial section, $\times 80$. 45, 46, CASG 60206: 45, transverse section, $\times 45$; 46, tangential section, $\times 40$. 47–49, CASG 60207: 47, transverse section, $\times 70$; 48, radial section, $\times 75$; 49, tangential section, $\times 45$.

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